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Overview and Synthesis

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Effects of Hurricane Andrew on Coastal and Interior Forests of Southern Florida: Overview and Synthesis

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ABSTRACT



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The effects of Hurricane Andrew upon the forests of south Florida as of early 1994 are summarized from studies conducted at sites located within the track of the storm as it passed across the peninsula. Updated information on the storm's track and eyewall configuration also is provided. Effects on slash pine savannas, hardwood hammocks, cypress domes and mangroves varied markedly but with some trends apparent. Severe damage and mortality of trees was greatest in mangrove forests where 59 to 85% of trees were killed, but vigorous seedling recruitment of red mangrove and sprouting of surviving black and white mangroves is now well underway. Severe effects in cypress domes was quite low, with only 4% mortality. In slash pine stands, over 80% of the trees were damaged, and mortality pattern was related to prior condition of the stands. Mortality in large, vigorous stands ranged from 17 to 24% but approached 100% in small remnant Miami rockridge pinelands located in developed eastern coastal areas. Tropical hardwood hammocks suffered extensive damage but only averaged 11.5% mortality and regrowth has been vigorous but not necessarily of the same species characterizing the pre-storm community. Overall mortality and damage increased with tree size except in hammocks where small trees were damaged or killed by limbs and crowns of larger trees. The extensive stands of exotic tree species were damaged but recovered quickly and vigorously. The potential of their expansion into hurricane-damaged habitats is one of several long-term concerns under investigation.

ADDITIONAL INDEX WORDS: *Mangrove forest, cypress dome, pinelands, hammocks, delayed mortality, coastal vegetation.*

INTRODUCTION

The southern end of the Florida peninsula (equatorward of approximately 26°N latitude; Figure 1), is a zone of transition between temperate and tropical biogeographic regions (SCHWARTZ, 1988; PLATT and SCHWARTZ, 1990). Rather than intermixing over the area, temperate and tropical plant species tend to segregate into different forested habitats. Along the coasts, in tidally influenced areas, mangrove forests occur, and at higher elevations, hardwood forests, both dominated by tropical species. In the interior lowlands of the peninsula, where forested habitats are located within extensive seasonal savannas (*sensu* SARMIENTO, 1984) and marshes, there are lowland stands of cypress (*Taxodium distichum*) commonly occurring as circular domes and hardwood swamp forests dominated by other temperate species such as *Persea borbo-*

nia, *Magnolia virginiana*, and *Ilex opaca*. On upland outcroppings of limestone at elevations of 1-10 m, there are South Florida slash pine (*Pinus elliotti* var. *densa*) savannas with large numbers of endemic plant species, as well as hardwood forests dominated by tropical trees and the warm temperate live oak (*Quercus virginiana*). General descriptions of these habitats, first compiled after 1900 (*e.g.*, HARPER, 1927; DAVIS, 1943), have been updated in the mid-1900s (LOVELESS, 1959; CRAIGHEAD, 1971) and most recently during the past decade (ODUM and McIVOR, 1990; SNYDER *et al.*, 1990; GUNDERSON and LOFTUS, 1993).

The climate of Southern Florida reflects its coastal and subtropical location (CHEN and GERBER, 1990). Precipitation is strongly seasonal; over 80% of the annual rainfall occurs during a wet season that typically lasts from June through November. In contrast, during the dry season, only occasional rains occur as a result of mixing of tropical oceanic air with cool continen-

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Figure 1. Track of hurricane Andrew across southern Florida on August 24, 1992. The center line denotes the track of the center of the eye. The two pairs of lines north and south of the center line delineate the width of the eyewalls as the hurricane crossed southern Florida. Numbers denote the following habitats: (1) mangrove forest, (2) cypress domes and strands, (3) Lostman's Pines (old-growth pine stands), (4) Long Pine Key (second-growth pine stands and subtropical hardwood hammocks), (5) sawgrass marshes, (6) tree islands (temperate swamp forests and subtropical hardwood hammocks), (7) urban development (Homestead, Florida), (8) main area of *Casuarina equisetifolia* invasion, (9) main area of *Melaleuca quinquenervia* invasion, (10) main area of *Schinus terebinthifolius* invasion of mangrove forests, (11) Elliott Key in Biscayne National Park, (12) Shark Slough in Everglades National Park, (13) Former agricultural land (Hole-in-the-Donut) invaded by *Schinus terebinthifolius*, (14) Florida Bay.

tal air masses that move across the peninsula. South Florida is also a region of extreme climatic events which have great ecological significance. In the dry season cold spells sometimes drop temperatures several degrees below freezing long enough to damage or kill cold sensitive tropical species (OLMSTED *et al.*, 1993). Extensive fires typically occur during the transition from dry to wet season (TAYLOR, 1979; DOREN and ROCHEFORT, 1984). Tropical storms and hurricanes may occur anytime during the wet season, and extreme ones may destroy forests and may profoundly alter the character of the landscape (GENTRY, 1974; CHEN and GERBER, 1990).

The purpose of this paper is to provide a synthetic overview of the impact of the most recent severe climatic disturbance, Hurricane Andrew, on the forested habitats of the southern tip of the Florida peninsula. Initial post-hurricane surveys indicated that the impact of Hurricane Andrew was greatest in forested habitats (OGDEN, 1992; PIMM *et al.*, 1994; LOOPE *et al.*, 1994; SMITH *et al.*, 1994). We provide general descriptions and summarize the state of seven forested ecosystems, four dominated by native tree species and three dominated by exotic tree species. We include representative photographs of these habitats at the time of and after the hurricane to illustrate direct, immediate changes that have occurred following the hurricane. We summarize quantitative descriptions of the effects of Hurricane Andrew based on field studies conducted from 1992–1994. Much of our data are taken from BALDWIN *et al.* (1995), NOEL *et al.* (1995), SLATER *et al.* (1995), SMITH *et al.* (1994), and PLATT *et al.* (1995). We use these data to compare patterns of hurricane damage in the different habitats and generate landscape-level hypotheses regarding effects of the hurricane on the forested ecosystems of southern Florida. Throughout, nomenclature follows TOMLINSON (1980).

HURRICANE ANDREW

Historical information for south Florida hurricanes begins in 1871 (GENTRY, 1974). Over the 85 year period from 1886 through 1970, 51 tropical cyclones crossed the approximately 250 km of the southern tip of Florida (SIMPSON and LAWRENCE, 1971). These included 33 hurricanes, 12 of which were severe (Category 3–5),

with maximum sustained winds over 200 km/h. Historically known frequencies translate into annual landfall probabilities of 0.09–0.16 (a hurricane) and 0.02–0.07 (a severe hurricane) in the south Florida region (GENTRY, 1974). Severe hurricanes that have affected south Florida habitats also affected by Andrew include ones that occurred in 1910, 1926, 1935 (the Labor Day hurricane), 1945, 1947, 1960 (Donna), and 1965 (Betsy). The longest interval between successive severe hurricanes was 27 years, between Betsy and Andrew.

Hurricane Andrew made landfall along the southeastern coast of Florida at 5:05 A.M. EDT on August 24, 1992 (RAPPAPORT, 1993), heading almost due west at a speed of approximately 16 km/h (STONE *et al.*, 1993). The eye of the hurricane crossed directly over Elliot Key in Biscayne National Park (Figure 1) with a storm surge of 3.2 m (10.5 ft) above mean sea level at the northern end and 2.0 m (6.7 ft) at the southern end, inundating the entire island. The highest surge, 5.2 m (16.9 ft), was an effect of the additive winds and lower barometric pressure nearer the northern eyewall and occurred just north of Elliot Key along the west coast of Biscayne Bay at Perrine, Florida. About the time that the eye of the hurricane crossed the west coast of Biscayne Bay, a minimum recorded central barometric pressure of 922 mb and maximum official sustained wind speeds of 232 km/h (145 mph) with gusts to at least 280 km/h (175 mph) were recorded (RAPPAPORT, 1993). Thus Hurricane Andrew was officially a category 4 on the Saffir/Simpson scale.

Even higher peak winds apparently occurred in the eyewalls of Hurricane Andrew. Maximum peak winds, resulting from tornadic wind structures and microbursts embedded within the hurricane, reached 340 km/h (212 mph) (FUJITA, 1992). Storm cells embedded within the hurricane created additive winds, causing short duration high peak wind velocities that caused the greatest damage (FUJITA, 1992). While in most hurricanes the eyewall to the right of the direction of movement (north in the case of Andrew) usually has the strongest winds, in Andrew both the front and rear eyewalls of the hurricane had peak winds comparable to the right eyewall.

Chronicles of wind speeds and storm surges fail to provide a complete understanding of the intensity of Hurricane Andrew. The following descriptions of storm damage from Florida Power

and Light Company (FPL) may help convey the level of damage resulting from this storm. During the 68 years prior to Hurricane Andrew that FPL had operated in southern Florida, no concrete power grid structure or poles had been lost. Their concrete structures and poles were engineered to withstand 300 km/h (190 mph) and 240 km/h (150 mph) sustained winds, respectively. During Hurricane Andrew FPL lost over 12% of its concrete power grid structures in Dade County; downed structures were located only within the path of the eyewall. In this same area, over 80% of the wooden service poles to homes were lost, and 100% of the wooden hi-voltage distribution lines were destroyed (J. Wong, *personal communication*).

Although the wind speeds of Hurricane Andrew were among the most intense ever recorded for hurricanes in south Florida, total rainfall was light (PIMM *et al.*, 1994). The width of the band of defoliated vegetation across the peninsula was narrow, about 50 km (PIMM *et al.*, 1994). Field surveys conducted shortly after the hurricane indicated that the most severe impact occurred in areas within the eyewalls of the hurricane (Figure 1) (OGDEN, 1992; LOOPE *et al.*, 1994).

We created a map of the track of Hurricane Andrew using National Weather Service (NWS) radar images taken every 18 minutes as the hurricane passed over southern Florida (Figure 1). The track of the eye and the eyewalls were compiled from radar images obtained by the NWS radar tracking station in West Palm Beach because the Miami NWS weather radar was destroyed when the eye of the storm made landfall at Elliot Key. We note that the path of the eye and eyewall delineated using the NWS radar images differs from those paths presented in other reports (*e.g.*, OGDEN, 1992; PIMM *et al.*, 1994; SMITH *et al.*, 1994). We present the methodology used to determine the path of the eye and eyewall so that comparisons can be made of the different techniques used to delineate the hurricane track across southern Florida. Precision is desirable given the narrow band of vegetation experiencing the highest wind speeds of the hurricane.

The fifteen individual maps were scanned using an optical color scanner and converted into a *t.i.f* file. They were then transferred to the Geographic Information System (GIS) located on a Sun Sparc II station. Using Image Tool the *t.i.f* file was converted to a raster image file, and exported directly into Geographic Resource Analysis and

Support System IV (GRASS IV) software program converting it into a cell file. Using first and fifteenth images we performed a resample in GRASS IV, using *r.resample* around the eye(s). A reclassification was performed to balance the separate color images and all the images were patched together. The combined images provided one theme showing the principal outline(s) and track of the eye and surrounding eyewall. The line images outlining the eyewall were traced using GRASS IV, *v.digit*. The resulting path is shown in Figure 1.

As is evident in Figure 1, examples of all the major forested ecosystems of the southern tip of Florida were located in the direct path of Hurricane Andrew. In Figure 2, three of the fifteen images are superimposed. From east to west, the images depict the storm at landfall along the west coast of Biscayne Bay, when the eye and left eyewall were over Long Pine Key in Everglades National Park, and when the hurricane was over the west coast of Florida. These images indicate that, as the hurricane crossed the peninsula, the intensity of the storm decreased; when it departed the west coast, it was a category 3 storm, with sustained winds of approximately 190 km/h (120 mph) around the eye (STONE *et al.*, 1993). A maximum storm surge of 4.6 m was recorded along the west coast of Florida (STONE *et al.*, 1993).

FORESTED HABITATS PRIOR TO HURRICANE ANDREW

Mangrove Forests

The approximately 270,000 ha of mangrove forests in Florida extend northward to about 29°N latitude in a narrowing coastal belt ranging from 15 to 0.1 km wide along both the Gulf of Mexico and Atlantic coasts (Figure 3) (ODUM and MCIVOR, 1990; GILMORE and SNEDAKER, 1993). The largest mangrove forests (Figure 1) occur along the southwest coast of the Florida peninsula (below 27°N latitude); 150,000 ha occur in Everglades National Park (OLMSTED and LOOPE, 1984). In addition, much narrower fringing mangrove systems are found along the west shore of Biscayne Bay and on offshore islands.

Three species, *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*, comprise mangrove forests in Florida. A fourth spe-



Figure 2. Composite radar image map of Hurricane Andrew at three positions in south Florida on August 24, 1992. The weather radar measures areas of relative storm strength from the radar beams scattered by raindrops and ice particles. The eyewall (the area of greatest radar scatter) of the hurricane, is the area of heaviest rain and highest winds, and is denoted by the yellow, green and blue colors surrounding the eye (white). Yellow and green colors farther to the north represent a large band of rain that was closer to the tracking station. The map was compiled using three of the fifteen images obtained from the National Weather Service radar tracking station in West Palm Beach, Florida. Right: landfall along the west coast of Biscayne Bay. Center: over Long Pine Key in Everglades National Park; Left: exiting the west coast. The path of the eyewall across south Florida was constructed by connecting the outer edges of high intensity colors around the eye using all fifteen images.



Figure 3. Mangrove forests (in Everglades National Park) along the west coast of Florida prior to Hurricane Andrew. Coastal halophytic prairie is in the foreground, and the Gulf of Mexico is in the background.

cies, *Conocarpus erecta*, not a true mangrove, commonly occurs in coastal areas where tidal inundation is reduced, as well in many non-tidal areas. Mangrove forests are divisible into several types based on tidal inundation rates, proximity to freshwater and substrate (LUGO and SNED-AKER, 1974; ODUM and MCIVOR, 1990). Although there is a tendency for zonation, the mangrove species intermix over many areas, particularly where hurricanes (LUGO and SNED-AKER, 1974, 1975), freezes (OLMSTED *et al.*, 1993) and lightning strikes (SMITH *et al.*, 1994) have occurred. *Laguncularia racemosa* and *A. germinans* readily sprout from roots or trunks following crown damage or bole breakage (BALDWIN *et al.*, 1995), but sprouting by *R. mangle*

is limited by the absence of dormant buds on branches older than three years (TOMLINSON, 1980).

Mangroves on both the east and west coasts have been repeatedly affected by hurricanes. Stands along Biscayne Bay were affected by major hurricanes in 1926, 1947, and 1965 (BALDWIN *et al.*, 1995). Stands along the west coast were influenced by major hurricanes in 1910, 1935, 1960 and 1965 (Figure 4) (SMITH *et al.*, 1994; CRAIGHEAD 1971). As a result, both east and west coast stands affected by Hurricane Andrew tended to be 25–30 yrs old and to resemble stands outside the path of Andrew that were last affected by hurricanes 25–30 yrs ago (BALDWIN *et al.*, 1994). In stands studied by



Figure 4. Mangrove forests (in Everglades National Park) that were last impacted by Hurricane Donna in 1960. Photograph was taken in the late 1960s, and shows regeneration of mangroves and standing dead mangroves killed by the hurricane. (Photo: L. Bancroft)

BALDWIN *et al.* (1995) *R. mangle* was the most abundant tree prior to Andrew, but there were scattered larger trees of *A. germinans* and *L. racemosa* that had survived previous hurricanes. Such surviving trees have provided evidence of mangrove growth potential in the absence of hurricanes. DAVIS (1940), ROBERTSON (1953), and CRAIGHEAD (1969) all found large surviving mangroves approaching or even exceeding one meter in diameter and about 25 m tall along the Gulf Coast. In contrast, most trees were 8–14 m tall in 10 yr-old post-Hurricane Donna stands on deeper Gulf Coast organic sediments (OLMSTED and LOOPE, 1974) and 11 m tall in 25 yr old post-1935 hurricane stands (CRAIG-

HEAD, 1971). In stands studied by BALDWIN *et al.* (1994), most *R. mangle* were less than 30 cm in diameter and were about 15 m tall; these stands were last impacted by Hurricane Betsy in 1965.

Cypress Domes

Cypress domes in southern Florida occur as monospecific stands of trees in poorly drained to almost permanently wet depressions of limestone bedrock (DUEVER *et al.*, 1984). Cypress also occurs as open stands of short trees (<4 m in height) in sawgrass marshes. The domes may occur in sawgrass marshes, as in much of Ever-

glades National Park, or they may be intermixed with pine savannas, as in Big Cypress National Preserve. The characteristic dome-shaped appearance (from a distance) results from the declining height of trees from the center to the periphery of the depressions (Figure 5). Most domes are small, ranging from <1 to 20 ha with 50–300+ trees ranging in size from 2 to 30 cm dbh (EWEL, 1990; NOEL *et al.*, 1995). At the time of the hurricane, most trees in these domes were small, with fewer numbers of trees being present in progressively larger size classes (NOEL *et al.*, 1994).

Slash Pine Savannas

South Florida Slash Pine savannas (dominated by *Pinus elliottii* var. *densa*) once covered about 75,000 ha of the coastal rock ridge (comprised of

Miami limestone) along the eastern border of the everglades sawgrass marshes. Only about 10% of this habitat is still present in southern Florida (SNYDER, 1986). The largest remaining intact remnant of the coastal ridge is approximately 8,100 ha mostly taken up by an area of Everglades National Park called Long Pine Key (Figure 1). About 4,600 ha of Long Pine Key are actually pine savannas (SNYDER, 1986). Other slash pine savannas are located on smaller, less continuous outcrops of Miami and Tamiami limestone in Big Cypress National Preserve (Lostman's Pines; Figure 1) and the lower Florida keys (SNYDER *et al.*, 1990).

South Florida Slash Pine savannas were described in the early literature as open, uneven-aged stands that included large trees up to 35 m tall and >100 yrs. The understory contained a diverse mixture of grasses, forbs, and shrubs, in-



Figure 5. Cypress dome in Everglades National Park, west of Long Pine Key. Larger trees are in the center, and smaller trees are around the periphery. (Photo: W.J. Platt)

cluding many endemic species (SNYDER *et al.*, 1990). Overwhelming evidence indicates that frequent, low intensity lightning-season fires (estimated to occur every 2–3 yrs by HARPER [1927]) occurred in these habitats (also see ROBERTSON, 1953, 1954; DOREN *et al.*, 1993).

Almost all South Florida Slash Pine savannas have been logged (SNYDER *et al.*, 1990). The major portion of the present slash pine forests on Long Pine Key in Everglades National Park (Figure 6) appears to have resulted from regeneration following extensive clearcuts in the 1930s and 1940s (DOREN *et al.*, 1993). Some areas in Long Pine Key remained unlogged but have been affected by extensive prescribed and escaped fires (DOREN *et al.*, 1993). Trees in these second-

growth stands typically were 50–60 yrs old at the time of Andrew. The only unlogged and non-fire managed stands of South Florida Slash Pine on limerock outcroppings occur in a region of Big Cypress National Preserve called Lostman's Pines (Figure 7). Trees in these old-growth stands varied from 5–10 yrs to >200 yrs old at the time of Hurricane Andrew (PLATT *et al.*, 1994).

The old- and second-growth stands at Lostman's Pines and Long Pine Key differed greatly in density and size-class structure at the time of Andrew (DOREN *et al.*, 1993). The average densities of pines was much greater, but with less variation in density in stands at Long Pine Key (1,147 trees/ha; range of 1,038–1,334) than at



Figure 6. Second-growth South Florida Slash Pine stand at Long Pine Key in Everglades National Park prior to Hurricane Andrew. (Photo: R.F. Doren)



Figure 7. Old-growth South Florida Slash Pine stand at Lostman's Pines in Big Cypress National Preserve prior to Hurricane Andrew. (Photo: R.F. Doren)

Lostman's Pines (673 trees/ha; range of 376–1,097). In addition, there were many fewer large trees at Lostman's Pines (average of 147 pines > 10 cm dbh per ha) than at Long Pine Key (755 pines > 10 cm dbh per ha). Moreover, the ranges of size classes was greater at Lostman's Pines than at Long Pine Key; there were both smaller and larger trees in the old-growth stands than in the second-growth stands at the time of Hurricane Andrew.

Hardwood Forests

Subtropical hardwood forests occur as inclusions in a number of habitats in the southern tip of the Florida peninsula. Locally called ham-

mocks, these forests occur on slightly elevated substrates in mangrove swamps, slash pine savannas (Figure 8), or as tree islands within drainages, such as Shark River Slough, that historically extended from Lake Okeechobee to Florida Bay and the Gulf of Mexico (SNYDER *et al.*, 1990). Nearly all tropical tree species, (*e.g.*, *Bursera simarouba*, *Lysiloma bahamense*, *Coccoloba diversifolia*, *Eugenia axillaris*), reach their northern distributional limits in the interior of the Florida peninsula on these tree islands. The various types of subtropical forests have been described by CRAIGHEAD (1971), OLMSTED and LOOPE (1974), and SNYDER *et al.* (1990).

Descriptions of hammocks at the time of Hurricane Andrew exist for those subtropical hard-



Figure 8. Subtropical hardwood hammock on Long Pine Key in Everglades National Park prior to Hurricane Andrew.

wood forests in the slash pine savannas of Long Pine Key (ROBERTSON and PLATT, 1992; SLATER *et al.*, 1994; SLATER and PLATT, in prep.). Although the frequency and intensity of fires in hammocks are much lower than in the surrounding pinelands and sawgrass (OLMSTED and LOOPE, 1974; OLMSTED *et al.*, 1983), fires do creep through hammocks during severe drought years. In 1989, a large lightning-initiated fire (the Ingraham Fire) burned through hammocks in the western end of Long Pine Key, killing stems of overstory trees back to the ground and resulting in greatly increased light levels (ROBERTSON and PLATT, 1992). This fire stimulated germination of seeds of some species

of trees (SLATER and PLATT, in prep.), while other species produced new shoots from suppressed buds on roots, boles or main branches. Hammocks burned in the Ingraham Fire had mostly very small stems, with scattered larger trees that survived the fire. There were more trees of all sizes >5 cm dbh in unburned hammocks. Data from three unburned hammocks (SLATER *et al.*, 1995) indicate that the largest numbers of stems occurred in the smallest size classes, with decreasing numbers in progressively larger size classes. Large trees (>30 cm dbh) were uncommon in all hammocks, but consistently were present. The largest trees in these hammocks were live oaks.

Exotic Tree Species

Southern Florida's island-like situation and recent emergence from the sea probably account for its high susceptibility to exotic plant invasions (MYERS, 1983; LOOPE, 1992). Three tree species, *Melaleuca quinquenervia*, *Schinus terebinthifolius*, and *Casuarina equisetifolia*, have already extensively altered native populations and communities in southern Florida (EWEL *et al.*, 1982; LAROSA *et al.*, 1992; LAROCHE and FERRITER, 1992). Aerial surveys conducted in 1993 by the South Florida Water Management District and Florida Division of Forestry established the following areas of invasion south of the northern rim of Lake Okeechobee: *M. quinquenervia*, 198,000 ha; *S. terebinthifolius*, 244,000 ha (not including Everglades National Park); and *C. equisetifolia*, 151,000 ha (FERRITER, *personal communication*). This survey included only natural areas and excluded urban, agricultural and coastal sites.

Schinus terebinthifolius

Over the past two decades, extensive areas of Gulf Coast mangrove forest in Everglades National Park have been colonized by *S. terebinthifolius*. Although established elsewhere in south Florida since the early 20th Century, the species was not prevalent until after 1960 (OLMSTED and YATES, 1984). Many Gulf Coast mangrove forests damaged by Hurricanes Donna and Betsy, as well as by freezes in 1977 and 1981 (LUGO and ZUCCA, 1977; OLMSTED *et al.*, 1993), have been invaded by *S. terebinthifolius* (Figure 9) (OLMSTED and YATES, 1984; SMITH *et al.*, 1994). As of 1987, 40,500 ha of Gulf Coast mangroves within Everglades National Park contained *S. terebinthifolius* (Figure 10). In former agricultural lands in sub-tropical Florida, densities in 10- to 20-year-old stands may exceed 6,000 individual trees/ha, and over 11,000 stems (<10 cm basal diameter) per ha. Forests older than 20 years have fewer trees (900/ha), but include many large (>10 cm basal diameter) stems (DOREN and WHITEAKER, 1990). Seeds of *S. terebinthifolius* ripen in December–February and are primarily bird dispersed.

Melaleuca quinquenervia

The spread of *M. quinquenervia* across the southern Florida landscape over the past three

decades has been explosive (LAROCHE and FERRITER, 1992). Invasion of *M. quinquenervia* in Everglades National Park has occurred principally along the eastern boundary in an area called the East Everglades (Figures 1 and 11). As of 1993 approximately 28,300 ha of the East Everglades contained *M. quinquenervia*, about 1,200 ha as monotypic stands. This species typically occurs either as individual outliers usually surrounded by seedlings or as dense monotypic stands (Figure 12). In young stands of 2–5 m tall trees, densities can reach approximately 2,000,000 trees/ha (DEVRIES and DOREN, 1992). *Melaleuca quinquenervia* flowers from July through January, and may flower up to five times per year (MESKIMEN, 1962). Individual mature trees may hold approximately 20 million wind-dispersed seeds, with capsules persisting on branches for >7 years (MESKIMEN, 1962).

Casuarina equisetifolia

Little is known of the expansion of *C. equisetifolia* into Florida. The species invades most vegetation types in southern Florida, but is particularly prevalent in coastal beaches and keys, where it was once planted, and in disturbed hammocks, short hydroperiod marshes and pinelands (LAROSA *et al.*, 1992). This nitrogen-fixing, non-leguminous angiosperm appears capable of altering soil nutrients in otherwise infertile soils (TORREY, 1976). Some coastal beaches and keys in Everglades National Park became dominated by *C. equisetifolia* within a decade after hurricanes Donna and Betsy (Figure 13). After an aggressive eradication program in the mid-seventies all *C. equisetifolia* in these sites was removed. At the time of Andrew, *C. equisetifolia* in Everglades National Park occurred as scattered populations in the East Everglades and in the southeastern corner of the park near Key Largo (Figure 14) (Everglades National Park, unpublished data).

EFFECTS OF HURRICANE ANDREW

Mangrove Forests

Mangrove forests on islands in Biscayne Bay and along the west coast of Biscayne Bay, especially in Biscayne National Park, received the full impact of high winds and tidal surges of the storm (Figure 15). Along the west coast (Figure 16),



Figure 9. *Schinus terebinthifolius* in mangrove forest (near Lostman's River in Everglades National Park) along the west coast of Florida prior to Hurricane Andrew. (Photo: R.F. Doren)

mangroves from Chatham River to Shark Point in Everglades National Park received the highest wind speeds and maximum tidal surges (SMITH *et al.*, 1994). The effects of Hurricane Andrew on mangrove forests along the west coast resembled those of Hurricane Donna in 1960 (Figure 17).

Hurricane Andrew damage in a number of mangrove forests on both the east and west coasts was described by SMITH *et al.* (1994). Along both coasts, damage was most severe within the eye and eyewalls and declined both to the north and south (SMITH *et al.*, 1994). One to two months after the storm, mortality among the three species was greatest in *R. mangle* and least in *A. germinans*. Mortality rates of *R. mangle* in

the 10 to 30 cm dbh size class exceeded 80%. Mortality was significantly lower for *A. germinans* than the other two species. Smaller size classes were less affected, with mangroves less than 5 cm dbh having only 10% mortality. Additional post-hurricane mortality of all three species occurred by July, 1993 (SMITH *et al.*, 1994). Such delayed effects were also noticed following Hurricane Donna (CRAIGHEAD and GILBERT, 1962; CRAIGHEAD, 1971). For all species, small trees regenerating in gaps formed by lightning strikes survived at higher rates than trees in surrounding areas (SMITH *et al.*, 1994).

In fringing mangrove forests along the west shore of Biscayne Bay, damage severity was strongly positively related to size for *L. racemosa*

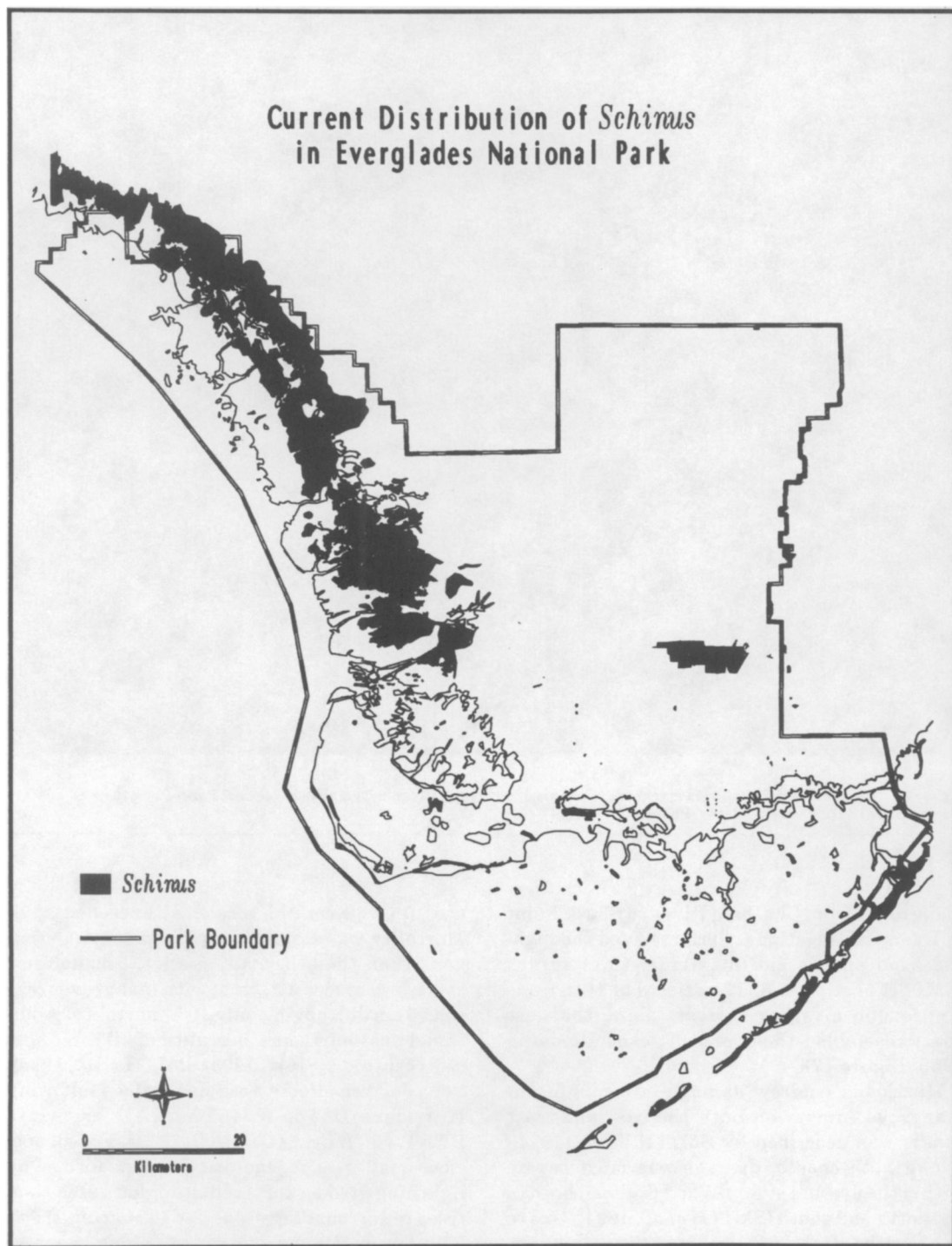


Figure 10. Map of *Schinus terebinthifolius* invasion of Everglades National Park compiled using 1987 aerial imagery.



Figure 11. *Melaleuca quinquenervia* stand in Everglades National Park prior to Hurricane Andrew. (Photo: D.D. DeVries)

and *R. mangle* but not for *A. germinans* (BALDWIN *et al.*, 1995). Nonetheless, species differed in type of damage; around 80% of *A. germinans* and *L. racemosa*, but only 50% of *R. mangle*, had snapped boles. In contrast, about 50% of *R. mangle*, but only about 20% of the other two species, lost branches or were leaning. Hurricane-related mortality (seven months after the storm) of *R. mangle* was 85% in sampled stands, compared to 65% for *A. germinans* and 59% for *L. racemosa*. Differences in mortality of the three species were most likely due to the absence of epicormic sprouting by *R. mangle*. Although most large trees of *A. germinans* and *L. racemosa* were severely damaged, many large trees of both species

survived and (as of 1.5 yrs later) had sprouts as much as one meter in length.

Along the fringing shorelines of Biscayne Bay at the time of the hurricane, densities of both seedlings and large trees of *R. mangle* much exceeded those of either *A. germinans* or *L. racemosa* (BALDWIN *et al.*, 1995). After the hurricane only scattered large *A. germinans* and *L. racemosa* tended to be present along with many seedlings of *R. mangle* (Figure 18). These seedlings grew rapidly; some had produced prop roots and even flowered by March, 1994. By March 1994, seedlings of *A. germinans* and *L. racemosa* also were present, but these were much smaller than those of *R. mangle*.



Figure 12. *Casurina equisetifolia* stand along Highland Beach on the west coast of Everglades National Park in 1973.

Cypress Domes

Both in Everglades National Park and Big Cypress National Preserve, about 75% of the cypress trees in domes up to more than 20 km from the center of the eye were damaged to some extent (NOEL *et al.*, 1995). The open savannas of short cypress trees were only slightly damaged by the storm. In the domes, only 4% of the cypress were severely damaged (snapped or uprooted trees), and only 12% of these severely damaged trees died (NOEL *et al.*, 1995). Maximum mortality was 4%, in a dome west of Long Pine Key located within the south eyewall. As in other forest types, larger trees experienced more severe damage and damage decreased with increasing distance from the center of the eye. Un-

like damage of mangroves, the decline in damage of cypress with increasing distance from the center of the eye was similar north and south of the eye (NOEL *et al.*, 1995).

Slash Pine Savannas

Almost all remaining South Florida Slash Pine stands on the Miami rockridge were directly in the path of Hurricane Andrew (Figure 1). Both second-growth stands at Long Pine Key (Figure 19) and old-growth stands at Lostman's Pines (Figure 20) were located within the eyewalls. In addition, almost all remnant stands located further east in Dade County also received the full impact of the storm as it made landfall. Almost all damage was restricted to pines; little

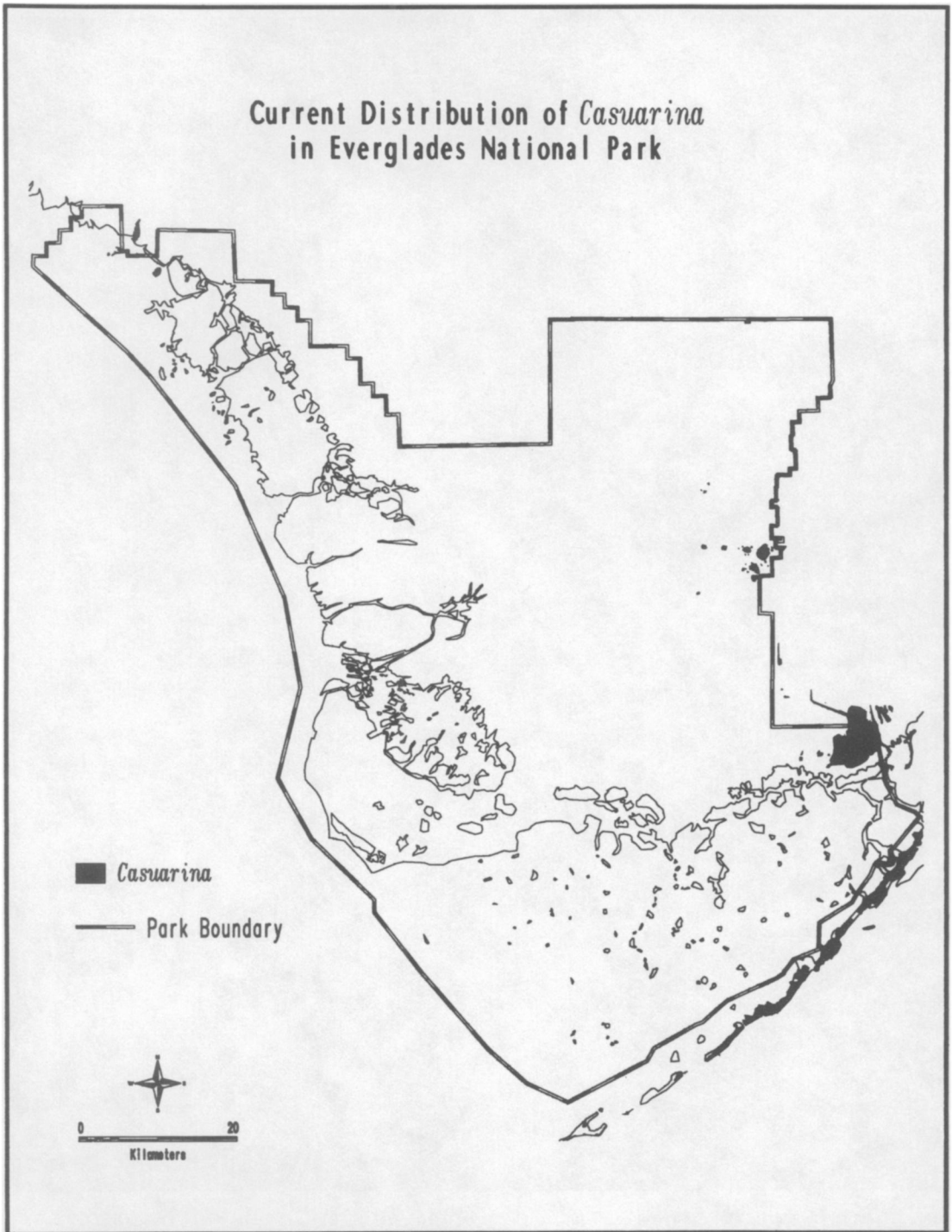


Figure 13. Map of *Casuarina equisetifolia* invasion of Everglades National Park compiled using 1987 aerial imagery.



Figure 14. Mangrove forest along the west coast of Biscayne Bay (Deering Estate) where the right eyewall made landfall and the tidal surge was >5 m. Photo taken six months after Hurricane Andrew. (Photo: W.J. Platt)



Figure 15. Mangrove Forest along the west coast of Florida (Broad River in Everglades National Park) where the left eyewall exited the coast and the tidal surge was approximately 2 m. Fringing mangroves along the riverfront in the foreground had higher survival than those in tidal flats in background. Photo taken six months after Hurricane Andrew. (Photo: T. Armentano)

damage occurred to understory shrubs or herbs (LOOPE *et al.*, 1994).

Assessments of direct mortality of pines from Hurricane Andrew have been made, both shortly after the hurricane and over time in research plots located in the same areas studied before the hurricane. Initial estimates, made in areas of Long Pine Key where access was possible, suggested mortality of about one-third of the pines (range 20–44%), with greater mortality of larger trees (LOOPE *et al.*, 1994). Data from randomly located plots collected four months after Hurricane Andrew, indicated an average of $24 \pm 2\%$ of the trees in Long Pine Key (range 5 to 45%), and $17 \pm 3\%$ of the trees in Lostman's Pines (range

3 to 40%) were directly killed by the hurricane (PLATT *et al.*, 1995). These data suggest that the initial surveys overestimated mortality in the second-growth stand on Long Pine Key, and that mortality was greater in second-growth than old-growth stands. Furthermore, mortality increased with tree size in both the old- and second-growth stands, but at much higher rates in the second-growth stands.

Over 80% of all pines, both on Long Pine Key and in Lostman's Pines, were overtly damaged by the hurricane (PLATT *et al.*, 1995). The proportion of trees experiencing severe damage was similar at both sites (11–17%). The severe damage category included trees with greater than



Figure 16. Mangrove forest along the west coast of Florida (Shark River in Everglades National Park) four months after Hurricane Donna. (Photo: F.C. Craighead)

half of the major crown branches lost and with boles leaning at an angle exceeding 45° or split from twisting. Nonetheless, trees tended to be more damaged in the second-growth stand at Long Pine Key. More trees experienced moderate damage on Long Pine Key (67%) than at Lostman's Pines (43%), and fewer trees experienced only minor damage at Long Pine Key (3%) compared to Lostman's Pines (33%). Four months after the storm, a larger proportion of severely damaged trees were dead at Long Pine Key (37%) than at Lostman's Pines (14%). This was especially the case for large trees (>10 cm dbh); of the large trees that were severely damaged 64% died at Long Pine Key, but only 14% at Lostman's Pines. Platt *et al.* (1995) suggest

that high densities of trees in Long Pine Key explain much of the increased damage and mortality in the second-growth compared to the old-growth stands. Trees were more likely to have abraded against one another in the second-growth stand during the hurricane, producing more damage.

In the fire-maintained pine savannas direct wind-related damage of trees could interact with other environmental forces, especially fire, so as to exacerbate hurricane effects. An initial assessment of increased fuel loads caused by Hurricane Andrew concluded that while fuel loads in pine-lands were increased, amounts were too small to significantly increase fire risk (LOOPE *et al.*, 1994). The initial survey did not consider, however, that surviving trees were damaged, in



Figure 17. *Rhizophora mangle* seedlings in mangrove forest along the west coast of Biscayne Bay (Snapper creek in Biscayne National Park) in the region where the right eyewall made landfall and the tidal surge was >4 m. Photo taken six months after the hurricane. (Photo: W.J. Platt)



Figure 18. Second-growth South Florida Slash Pine stand (Block I) where the left eyewall passed over Long Pine Key in Everglades National Park. Photo taken six months after the hurricane. (Photo: W.J. Platt)

many cases extensively. Fires soon after a severe hurricane might accentuate the stress on such trees. Mortality might be increased, particularly as a result of local fuel loads (crowns and boles that have fallen at the bases of surviving trees) or of bole damage resulting in sap extrusion (and thus increased likelihood that fires will burn into the trunk and that cambium temperatures will reach lethal levels).

Only one prescribed fire was conducted in the Long Pine Key pine savannas after Andrew. In a 5 ha site in eastern Long Pine Key that was burned 2 months after the hurricane, pine mortality was 50%, more than twice that in the rest of Long Pine Key (Figure 21). Severe fire damage also has been reported in pine savannas (and

other subtropical habitats) following hurricanes (WOLFSSON, 1967; WHIGHAM *et al.*, 1991), as well as in vegetation types of several kinds in south Florida following hurricanes or freezes (CRAIGHEAD, 1971; WADE *et al.*, 1980). The results of the trial fire, the presence of large numbers of trees with trunk damage and sap on the trunk, as well as documentation of high pine mortality following other severe disturbances, led to suspension of the Long Pine Key prescribed burn program during 1993–1994. No lightning-initiated fires occurred following the hurricane in 1992 or during 1993. Trial fires are scheduled for the early wet season of 1994 in some areas of pines outside the large contiguous pine savannas of Long Pine Key.

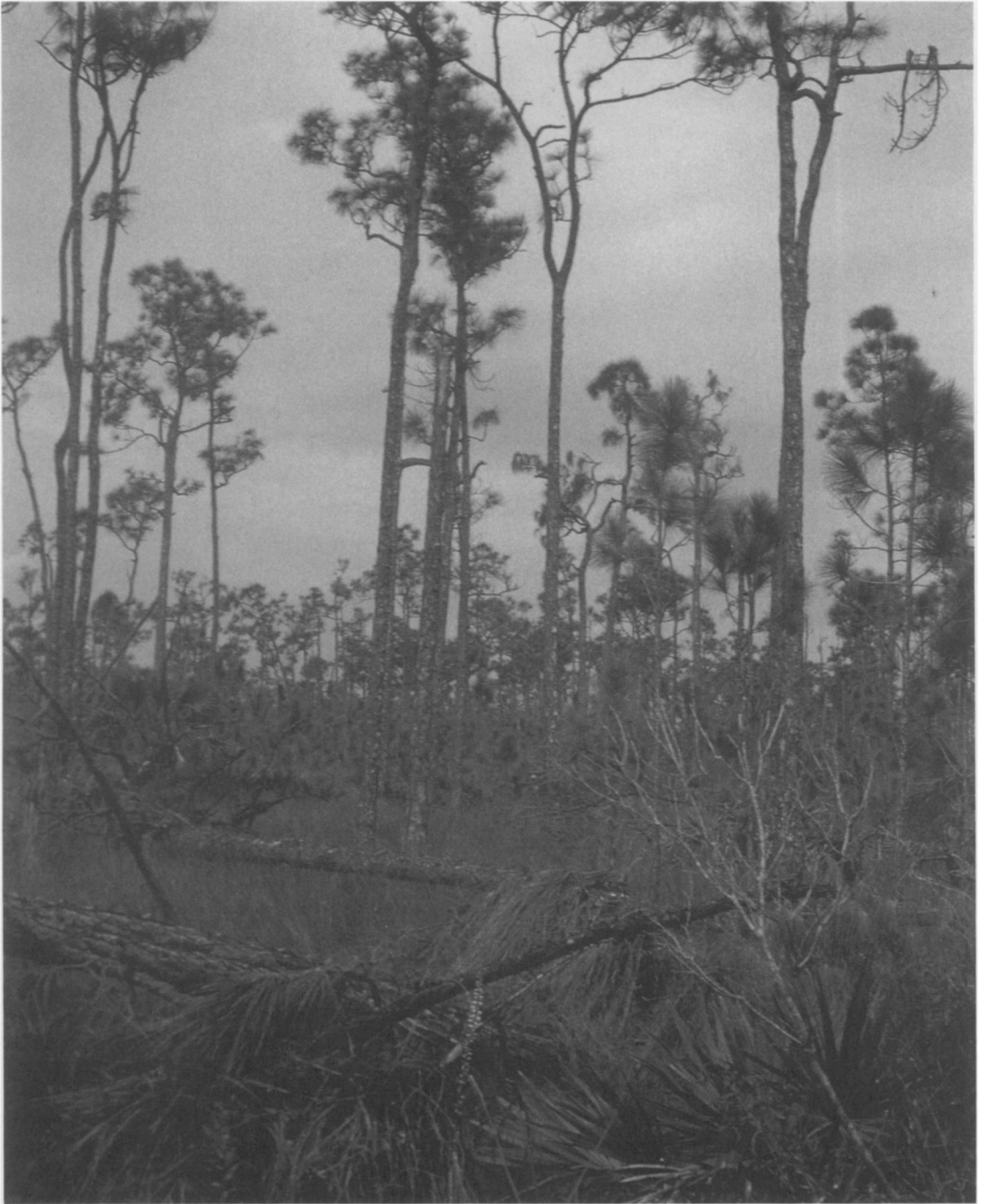


Figure 19. Old-growth South Florida Slash Pine stand where the right eyewall passed over Lostman's Pines in Big Cypress National Preserve. Photo taken six months after the hurricane. (Photo: W.J. Platt)

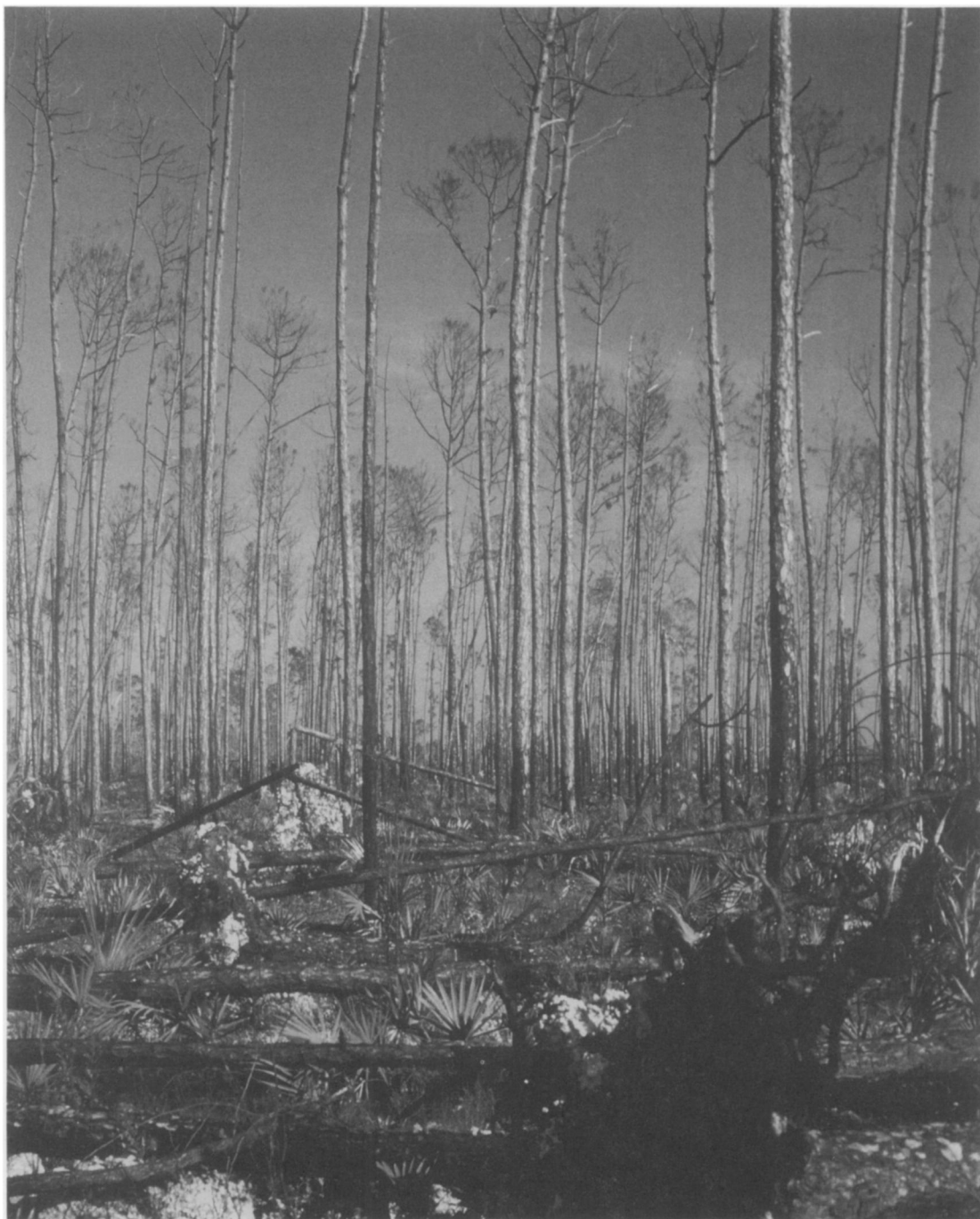


Figure 20. Second-growth South Florida Slash Pine stand (Pine Island in Everglades National Park) burned October 1992, two months after the hurricane. Photo taken six months after the hurricane. (Photo: W.J. Platt)



Figure 21. Second-growth South Florida Slash Pine stand (Navy Wells) east of Everglades National Park 16 months after Hurricane Andrew. Stand was last burned in 1992 before the hurricane. (Photo: W.J. Platt)

Although effects of insects (especially bark beetles) on pines following hurricanes have been reported as minor (see WILKINSON *et al.*, 1978), severe wind damage, coupled with effects of long-term declines in stand vigor, can result in susceptibility of pines to insect outbreaks. The proportion of trees in the severely damaged class was up to four times greater in the remnant stands sampled (Navy Wells, Deering Estate) than in Long Pine Key or Lostman's Pines (Platt, Doren and Armentano, unpublished data). By June 1993, at the beginning of the wet season, insect outbreaks accompanied extensive mortality of pines in many remnant rockridge pinelands in Dade County east of Everglades National Park. As of April, 1994, slash pine mortality ranged from 75 to 100% in virtually all of these stands (Figure 22).

The greater damage to trees in the remnant pine stands may be traceable to long-term decline in stand vigor associated with their location in an intensively urbanized or agricultural landscape. Large-scale drainage has lowered ground-water levels 0.6–1.2 m over large areas. In addition, it is unlikely that any of these stands has experienced a natural fire regime in many decades. Fires have been either absent or sporadic, but those that have occurred have been severe enough to kill young pines. This has led to a proliferation of hardwoods that retard flammability except under severe drought conditions. Some combination of these various influences may have increased susceptibility to insect attacks (*e.g.*, lowered ability to produce pitch). A similar suggestion was made by CRAIGHEAD (1978) regarding slash pine mortality along the southwest coast of Florida; he postulated that a combination of moisture stress, lack of fire (and thus proliferation of hardwoods, which reduced water availability to pines), and the spread internally of a fungus introduced into trees by pine bark beetles caused mortality of large pines during a severe drought year.

As of April 1994, greatly increased post-hurricane mortality of the large slash pine stands in Long Pine Key and Lostman's Pines has not occurred (Figure 23). A resurvey of those plots sampled to estimate mortality four months after Andrew (January, 1993), revealed that on the average approximately 7% additional mortality has occurred between January, 1993, and January, 1994 (Platt, Doren, Armentano, unpublished data). The additional deaths were mostly of trees

initially classified as severely damaged. Low rates of delayed mortality even several years following a hurricane have been documented for an old-growth longleaf pine stand (PLATT and RATHBUN, 1994). Thus, low rates of continued mortality may well occur for a number of years in the old- and second-growth stands in Lostman's Pines and Long Pine Key.

Slash pine regeneration in both the old-growth stands in Lostman's Pines and the second-growth stands in Long Pine Key was occurring at the time of Hurricane Andrew. Stands in both sites contained numerous small trees not yet 1.5 m tall. The limited mortality of large trees in both the old- and second growth stands is likely to result in a pulse of recruitment of small trees (*i.e.*, into height growth stages) over the next several years. Except in these two areas, natural regeneration appears very limited because of inadequate seed sources and site dominance by hardwoods.

Subtropical Hardwood Hammocks

In three Long Pine Key subtropical hardwood hammocks (not recently burned) sampled four months after the storm by SLATER *et al.* (1995), virtually every tree sustained extensive to entire defoliation (Figure 24). Such complete defoliation was commonplace in hammocks within the eye or eyewall, but the extent of defoliation decreased rapidly away from the track of the eye of the storm (LOOPE *et al.*, 1994). Damage resembled that from Hurricane Donna in 1960 (Figure 25).

In addition to defoliation, the canopies of hammocks within the eye and eyewalls of Hurricane Andrew were removed. In the hammocks studied by SLATER *et al.* (1995), about 85% of all hammock trees >2 cm dbh incurred major damage (loss of major branches, leaning at angles of 25–75° from the ground, snapped below major branches, or downed [including trees uprooted and/or leaning at angles <25° from the ground]). About 46% of the damaged trees were snapped, while only 9% were downed. This pattern of damage most likely resulted from the trees being anchored in limerock, and thus not readily uprooted.

Hurricane-induced tree mortality four months after the storm averaged 11.5% (SLATER *et al.*, 1995). There was a negative relationship between tree size (dbh) and mortality. Mortality of small trees (<6 cm dbh) was 13.9%, declining to 3.9%

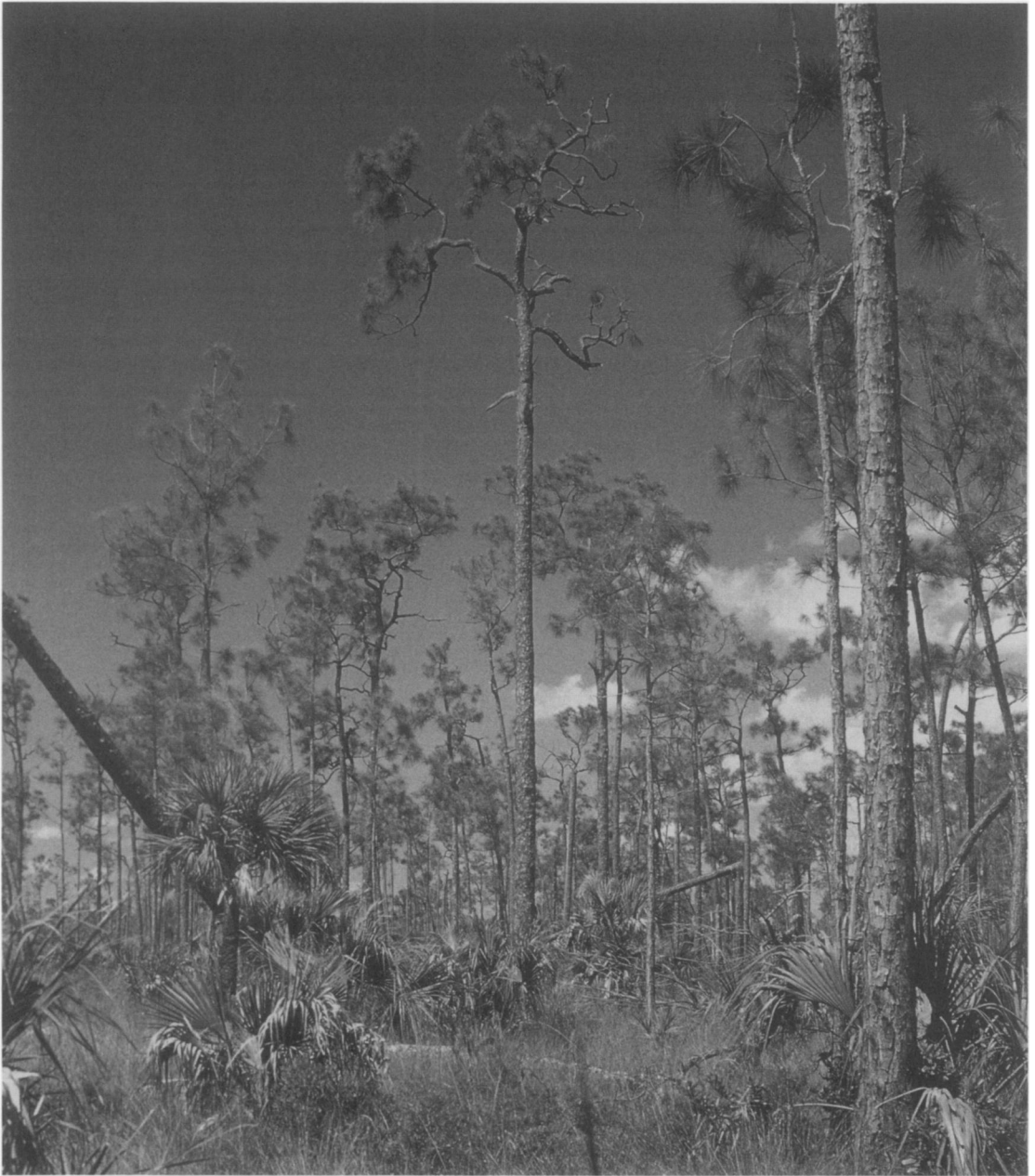


Figure 22. Old-growth South Florida Slash Pine stand at Lostman's Pines 18 months after Hurricane Andrew. (Photo: W.J. Platt)

of trees exceeding 30 cm dbh. Snapped trees in small size classes comprised a larger proportion of the mortality than expected. Smaller trees were more likely to die if snapped than larger

trees because the former commonly were buried beneath the crowns and branches of larger neighbors, while boles and stumps of larger trees were more likely to be exposed. In addition, larger



Figure 23. Subtropical hardwood hammock (#113, Block B) where the left eyewall passed over Long Pine Key. Photo taken four months after the hurricane. (Photo: W.J. Platt)

trees were more likely to be debranched rather than snapped, and many of these resprouted.

The pattern of extensive damage, but low mortality that occurred within the eye and eyewall was strikingly uniform in all hammocks studied by SLATER *et al.* (1995). These general patterns have been reinforced by our observations on other hammocks as well. Essentially all the canopy was removed, and all trees were defoliated. Mortality was low, especially among large trees. Hence, there were no large gaps in the sense suggested by LOOPE *et al.* (1994). Instead, entire hammocks underwent an instantaneous transformation (also see BOUCHER *et al.*, 1990) from closed-canopy forest to one large opening in which light penetrated throughout the subcan-

opy. The forest floor was buried, however, beneath tremendous masses of dead vegetation. In addition, defoliated and damaged trees rapidly produced new shoots from suppressed buds on canopy branches, boles, and/or roots. By one year post-hurricane the new shoots were commonly one meter or more in length. Only where trees were uprooted and no other vegetation fell on the root mass (and exposed limerock beneath) were there bare patches of ground present. As a result, while seeds of species with buried seed pools in the soil (*e.g.*, *Carica papaya*, *Trema micrantha*, *Lysiloma bahamense*) did germinate in some bare areas left by tip-ups of large trees, there was no massive germination response of such species. Changes in the composition of ham-



Figure 24. Subtropical hardwood hammock (Mahogany Hammock) four months after Hurricane Donna. Large tree standing in background is *Swietenia mahagoni*. (Photo: F.C. Craighead)

mock vegetation will, if the resprouting trees continue to survive and regrow, be minimal, and recovery of pre-hurricane vertical structure should occur rapidly.

While arboreal hammock vegetation has shown a marked tendency to recover from the hurricane damage, other species took advantage of the transient removal of the canopy in these seasonal subtropical forests. One herbaceous species, *Ipomoea acuminata*, germinated *en masse* in many hammocks and grew rapidly, forming dense tangles covering downed vegetation within a year after Andrew. In addition, understory species (e.g., *Ardisia escallonioides*, *Eugenia axillaris*, *Exothea paniculata*), although seldom flowering

beneath closed canopies, have flowered extensively in the two years following the hurricane.

Exotic Tree Species

No quantitative information presently is available on the impact of Hurricane Andrew on forests dominated by any of the three major exotic species. Observations by the authors, and by SMITH *et al.* (1994), indicate that large areas of forests of all three species were severely damaged, and trees were completely defoliated. Rapid resprouting of the exotics occurred, as in other subtropical hardwoods. Today, forests dominated by exotic species appear to be recov-



Figure 25. Subtropical hardwood hammock (Royal Palm Hammock) where the left eyewall passed over Long Pine Key. Photo taken seven months after the hurricane. Standing trees in background are *Bursera simarouba*. (Photo: W.J. Platt)

ering rapidly. Current research is being conducted to evaluate the potential spread of these exotic species in various hurricane impacted and unimpacted communities throughout the area.

While *Schinus terebinthifolius* trees bore few seeds during the hurricane, the potential for long-distance seed dispersal by birds in post-Andrew environments makes this species perhaps the most serious exotic plant now threatening native communities within south Florida. The west coast area most affected by Hurricane Andrew (Figure 1) lies within the northern end of the hurricane damaged area and immediately south of the densest infestations of *S. terebinthifolius* in Everglades National Park. OLMSTED and YATES (1984) have hypothesized that hurricanes

and freezes have provided suitable sites for establishment of *S. terebinthifolius*. At this time, however, there are no indications of massive *S. terebinthifolius* invasions as a result of Hurricane Andrew. However, large areas of dead and damaged mangroves still are present, possibly resulting in extended opportunity for future colonization.

The principal damage to *Melaleuca quinque-neria* forests was loss of leaves and branches and blowdowns. Nonetheless, the branchless boles of the trees (even those that were blown down) quickly resprouted and have produced fruit. In addition, Hurricane Andrew presumably dispersed seed and seed capsules of *M. quinque-neria* along its entire track across southern

Florida. However, seedling germination and survival following disturbances depends on a combination of favorable conditions (MYERS, 1975, 1983). While *M. quinquenervia* is known to spread rapidly (following intense fire for example), it does not always do so. Specific soil moisture conditions and water levels are critical for the "waves" of expansion of *M. quinquenervia* that can occur over hundreds and often thousands of acres in a single event (MYERS, 1975, 1983). These conditions do not appear to have occurred after Hurricane Andrew; no massive seedling invasions have been observed. However, it is most likely that outliers (resulting from the establishment of individual seedlings) will occur because suitable conditions for seedling establishment very likely were available in some sites. As a result, *M. quinquenervia* may invade previously uncolonized areas, increasing its potential spread in south Florida (MOODY and MACK, 1988; WOODALL, 1982).

Damage to, and recovery of *Casuarina equisetifolia* forests was very similar in pattern to *M. quinquenervia* forests. As with *M. quinquenervia*, seeds of *C. equisetifolia* probably were spread along the track of the hurricane. To date, no reinvasion of coastal areas or keys previously cleared of *C. equisetifolia* appears to be occurring as a direct result of the hurricane. In addition, new invasion locations have not been observed. Characteristics of *C. equisetifolia* seed viability and longevity are unknown. Given its nitrogen fixing ability, however, these low nutrient sites will probably remain susceptible to *C. equisetifolia* invasion as long as the effects of the disturbance from the hurricane persist.

DISCUSSION

General Patterns

Trees were damaged and killed to at least some extent in all the forested habitats along the track of Hurricane Andrew in south Florida. Damage was restricted principally to forests located within the eyewalls and effects diminished rapidly with increasing distance from the path of the eyewall (NOEL *et al.*, 1994; SMITH *et al.*, 1994).

Within the narrow path of the eyewall both the severity of damage and direct mortality varied considerably among habitats. The greatest damage and mortality occurred in mangrove forests, which experienced high winds, tidal surges, and

probably the greatest alterations of the physical environment (*e.g.*, sediment scouring and deposition, high salinities, *etc.*; see SMITH *et al.*, 1994; BALDWIN *et al.*, 1995). In hardwood hammocks wind damage was as severe as in the mangroves, but mortality was much lower. Based on our field observations, patterns of damage and mortality in forests of exotic hardwoods resembled those in the native hardwood forests. In pine savannas, where major effects also were a result of high winds, tree mortality rate resembled that in hardwood hammocks, but severe damage was lower in the hardwood forests. In cypress domes, most trees experienced some damage from winds, but both severe damage and mortality were uncommon.

Mortality also varied considerably within certain habitats. Where average mortality was either very high (*i.e.*, mangroves) or very low (*i.e.*, cypress domes), relatively little variation in mortality occurred compared to habitats with intermediate mortality. In both the pine savannas and hardwood hammocks, mortality was not catastrophic, but varied spatially depending on localized effects. Some localized higher mortality of trees almost certainly resulted from the occurrence of tornadic winds and microbursts described by FUJITA (1992). Other localized higher mortality resulted from interactions among trees. In the hammocks, larger trees fell upon smaller trees, causing higher mortality of the smaller trees than where the limbs and boles did not fall. In the pine savannas, especially in the dense second-growth stands, trees were likely to fall on adjacent trees, causing higher mortality.

In most habitats mortality related strongly to tree size. Mortality increased with size in mangroves, pinelands and cypress but actually decreased with size in hammocks. The divergent pattern for hammocks reflected the tendency for big trees to fall on little ones and kill them. In mangroves, size effects related to the relatively small and even-aged tree populations. In the pine savannas, the open canopy, narrow crowns and patchy stem distributions influenced mortality patterns.

All of the forests studied within the eyewalls with the possible exception of the cypress domes, had been subjected to disturbances in the past half-century or so. Consequently, forest response derived partly from the altered stand structure at the time of the storm. When Hurricane Andrew hit, mangrove forests consisted of rela-

tively even-aged, small diameter individuals with only a scattering of larger stems of *L. racemosa* and *A. germinans*. This distribution, as well as the numerical abundance of smaller *R. mangle*, appears to have represented continuing recovery from the effects of Hurricanes Donna and Betsy. Present evidence suggests that this pattern will continue. The life cycles of mangroves appear to reflect two different mechanisms for regeneration in post-hurricane environments. Large trees of *R. mangle* suffer high mortality, but seedlings and small juveniles not only survive at high rates but are very precocial in the post-hurricane environment. In contrast, sizable proportions of the large trees of *L. racemosa* and *A. germinans* survive hurricanes and resprout, growing rapidly in the post-hurricane environment.

Thus mangrove forests appear resistant to structural change even if exposed to severe hurricanes every few decades as long as environmental conditions are not severely altered. That such severe alterations sometimes occur, however, is suggested by the absence of mangrove regeneration in formerly forested salt prairies shorn of trees by earlier hurricanes and by the replacement of black mangroves stands near Flamingo by red mangroves after the 1935 hurricane (CRAIGHEAD, 1971; SMITH *et al.*, 1994). Such departures, however, appear to be local in scale and may not represent long-term change.

In a similar vein, the effects of Hurricane Andrew on the old- and second-growth slash pine savannas reflected the prior history of logging and fire management and of the intensive development of the eastern coastal areas. Size-class distributions of pines and the spacing of stems throughout the stand are changed by human intervention and seem to influence hurricane responses. The much reduced area of the pineland ecosystem type as a whole epitomizes the fact that never before in south Florida has a severe natural disturbance been superimposed upon a landscape so profoundly altered by human impacts. As a result, neither the impact of the hurricane, nor the post-hurricane changes in the habitats, represent only natural processes. This is especially true for small, isolated upland forest remnants, although larger preserves (such as Everglades National Park and Big Cypress National Preserve) are not exempt from the possibility of effects resulting from the interactions of natural and human disturbances of the environment. Continued study of the damaged hab-

itats will be necessary to fully understand the hurricane's enduring effects including the possibility that the modern south Florida ecosystem will respond differently than it would have under undisturbed conditions.

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